

The Morphology and Mechanics of Octopus Suckers

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Abstract. The functional morphology of the suckers of several benthic octopus species was studied using histology and cinematography. The suckers consist of a tightly packed three-dimensional array of musculature. Three major muscle orientations are found in the wall of the sucker: (1) radial muscles that traverse the wall; (2) circular muscles that are oriented circumferentially around the sucker, including a major and minor sphincter muscle; and (3) meridional muscles that are oriented perpendicular to the circular and radial muscles. The connective tissue of the sucker includes inner and outer fibrous connective tissue layers and an array of crossed connective tissue fibers embedded in the musculature of the sucker.

Attachment is achieved by reducing the pressure inside the sucker cavity. We propose the following mechanism to explain this pressure reduction. Contraction of the radial muscles thins the wall and thus increases the enclosed volume of the sucker. If the sucker is sealed to the substratum, however, the cohesiveness of water resists this expansion. Thus, contractile activity of the radial muscles reduces the pressure of the enclosed water. The radial muscles are antagonized by the circular and meridional muscles so that the three-dimensional array of muscle functions as a muscular-hydrostat. The crossed connective tissue fibers of the sucker may store elastic energy, providing a mechanism for maintaining attachment over extended periods.

Introduction

Octopus suckers perform a remarkable variety of functions. Packard (1988) listed six distinct roles of the suckers of benthic octopuses including: (1) locomotion; (2) anchoring the body and holding prey; (3) sampling, col-

lecting, and manipulating small objects; (4) chemotactile recognition; (5) displays; and (6) cleaning maneuvers. These diverse roles demand that the suckers be flexible and dexterous yet capable of generating large forces (see Dilly *et al.*, 1964). Previous research has focussed on the chemotactile ability of the suckers (see Wells, 1978), on the sensory receptors of the suckers (Graziadei, 1962; Graziadei and Gagne, 1976a, b), and on their morphology (see below). Our understanding of how the sucker generates the movements that allow it to manipulate and forcefully grip objects is incomplete.

The morphology of octopus suckers has been described previously. Nixon and Dilly (1977) described the surface features of octopus and squid suckers from different genera. The sucker musculature has been described by Girod (1884), Guérin (1908), Nachtigall (1974), Niemiec (1885), and Tittel (1961, 1964), but the proposed mechanisms of action are incorrect both in their analysis of the function of the musculature and in understanding the ability of water to sustain sub-ambient pressures. Previous studies also overlooked important features of the connective tissue.

The suckers are muscular-hydrostats as defined by Kier and Smith (1985) (see also Smith and Kier, 1989). The musculature is arranged in a tightly packed, three-dimensional array that provides the skeletal support and the force for movement. This type of system produces movements that are localized and remarkably complex, allowing precise changes in shape by bending, contracting, or stretching at any point. In this paper we describe the muscle arrangements in the suckers of several octopus species and discuss the function of these arrangements.

Materials and Methods

Experimental animals

Specimens of *Eledone cirrosa* were supplied by The Laboratory of the Marine Biological Association of the

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United Kingdom, Plymouth. Specimens of *Octopus joubini* and *Octopus maya* were supplied by The Marine Biomedical Institute of the University of Texas Medical Branch at Galveston, Texas. Specimens of the *Octopus bimaculoides/bimaculatus* complex (see Pickford and McConnaughey, 1949) were supplied by Pacific Bio-Marine, Venice, California, and Chuck Winkler Enterprises, San Pedro, California. Observations of sucker behavior and kinematics were made primarily on *O. bimaculoides/bimaculatus* and *O. maya*. A detailed morphological analysis of the suckers was performed on specimens of *E. cirrosa*, *O. joubini*, and *O. bimaculatus/bimaculoides*.

Histology

Blocks of arm tissue that included several suckers were obtained from freshly killed animals that were anesthetized in 1% ethanol in seawater. The tissue was fixed in Bouin-Dubosq fixative (Humason, 1979) or in 10% formalin in seawater for 24–48 h. In some cases, blocks of tissue were obtained from specimens that had been fixed whole in 10% formalin in seawater after anesthesia. The tissue was dehydrated in ethanol and embedded in paraffin (MP 56°C). The blocks were sectioned serially at 5–10 μm on a rotary microtome. Serial sections were made in three mutually perpendicular planes. The sections were stained using one of the following techniques: (1) Mallory's triple stain as outlined by Pantin (1946); (2) Milligan trichrome stain; (3) Picro-Ponceau with iron hematoxylin; or (4) Mowry's colloidal iron method. The procedures followed for stains 2–4 above are outlined by Humason (1979). Sections were examined with bright-field, phase contrast, and polarized light microscopy.

Computer-assisted three-dimensional reconstruction

The extrinsic musculature of the suckers of one specimen of *E. cirrosa* was examined using a computer program for three-dimensional reconstruction (PC3D Three-Dimensional Reconstruction Software, Jandel Scientific, Corte Madera, California). Serial frontal sections (see description of section planes below) 10 μm thick were used for the reconstructions. The outlines of the major muscle groups of every fourth section were traced using a camera lucida on a compound microscope. Alignment of the series of tracings was performed according to the visual best-fit method (Gaunt and Gaunt, 1978; Young *et al.*, 1985). The tracings were then digitized with a Numonics 2210 digitizing tablet. The PC3D software, running on a CompuAdd 286/12 AT microcomputer, stacked the outlines of specified muscle bundles from each section, producing a three-dimensional representation of the muscular morphology that could be viewed in any orientation. The reconstructions

shown in Figure 8 were plotted on a Hewlett-Packard HP 7475A plotter.

Cinematography

A specimen of *O. maya* was filmed walking on a glass aquarium wall with a Canon Scoopic 16mm movie camera filming at 48 frames/s using Eastman Ektachrome Video News Film. The film was viewed frame by frame on an L-W International film analyzer, and calipers were used to measure the diameter of the sucker and the diameter of the opening to the acetabulum. The measurement error was <5%. Measurements were made from one 100-ft roll of film, choosing every sucker (total of 26 suckers) that attached or released and whose outlines were distinct enough to measure. Suckers attached to the glass could be distinguished because they remained stationary relative to the movement of the arm.

Results

Gross morphology of the suckers

The gross morphology of the suckers of different octopus species has been described previously (Girod, 1884; Guérin, 1908; Niemiec, 1885; Nixon and Dilly, 1977; Packard, 1988), and a brief summary of observations on the species we examined is provided here. The sucker consists of two general regions: the acetabulum and infundibulum (Girod, 1884) (Fig. 1). The infundibulum is the exposed portion of the sucker that is applied to the substratum during attachment. The acetabulum is a more or less spherical cavity that opens to the infundibulum through a constricted orifice (Fig. 1). The surface of the infundibulum bears a series of radial grooves and ridges while the surface of the acetabulum is smooth. The sucker is covered by a chitinous cuticle or sucker lining (see below) that is particularly well-developed on the infundibulum. The sucker lining is shed periodically and renewed continuously (Girod, 1884; Naef, 1921–1923; Nixon and Dilly, 1977; Packard, 1988). The infundibulum is encircled by a rim covered with a deeply folded, loose epithelium. The suckers are attached to the arms by a short muscular base that is covered by a continuation of the dermis and epidermis of the arms. A single row of suckers is present on the arms of *E. cirrosa* and two rows of suckers are present on the arms of the *Octopus* species.

Sucker microanatomy

For the purposes of this discussion, we refer to transverse and frontal sectional planes. Transverse sectional planes are defined as sections perpendicular to the long axis of the arm. Frontal sections are parallel to the plane defined by the opening of the sucker.

Intrinsic sucker musculature. Although we did not

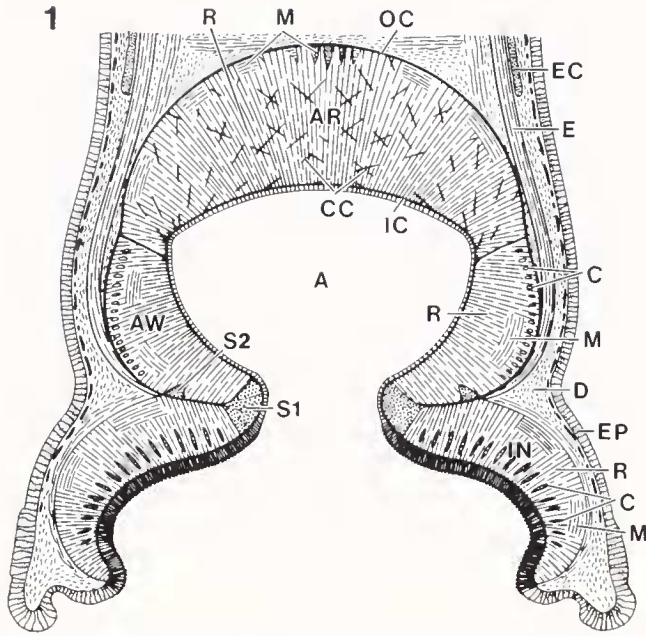


Figure 1. Schematic diagram of the microanatomy of the sucker of *Octopus* in transverse section. A, acetabulum; AR, acetabular roof; AW, acetabular wall; C, circular muscle; CC, crossed connective tissue fibers; D, dermis; E, extrinsic muscle; EC, extrinsic circular muscle; EP, epithelium; IN, infundibulum; IC, inner connective tissue layer; M, meridional muscle; OC, outer connective tissue layer; R, radial muscle; S1, primary sphincter muscle; S2, secondary sphincter muscle.

make a systematic study of a wide range of sucker sizes and sucker locations on the arms, the general arrangement of the muscle and connective tissue of the suckers is the same for the different species and sucker sizes we examined. Several minor differences between genera were observed and are noted below. The acetabular and infundibular portions of the sucker consist primarily of a tightly packed, three-dimensional array of muscle fibers. The muscle fibers can be categorized by orientation into three major groups: radial muscle fibers that extend across the wall of the sucker more or less perpendicular to the inner surface; circular muscle fibers that are oriented circumferentially around the sucker and parallel to the frontal plane; and meridional muscle fibers that are oriented perpendicular to the radial and circular muscle fibers (Fig. 1).

The acetabular portion consists of a wall region and a domed roof. The acetabular wall includes radial, circular, and meridional muscle fibers. The acetabular roof includes radial and meridional muscle fibers but lacks circular muscle fibers. Radial muscle fibers extend between their origins and insertions on an inner fibrous connective tissue layer lining the acetabulum and an outer fibrous connective tissue layer encapsulating the sucker (Figs. 1–3). As the radial fibers project toward the outer surface, they interdigitate with bundles of meridional muscle fibers. In the acetabular wall, the radial mus-

cle fibers also interdigitate with circular muscle bundles (Fig. 2). The circular muscle bundles extend around the perimeter of the acetabular wall.

The location of the circular and meridional muscle bundles in the acetabular wall of the suckers of *Eledone cirrosa* is different from that of the *Octopus* species examined in this study. In *E. cirrosa*, the meridional muscle bundles are located peripheral to the circular muscle bundles. In the *Octopus* species, however, the arrangement is reversed; a distinct series of circular muscle bundles are located peripheral to the meridional muscle bundles (Compare Figs. 1 and 2).

In addition to the circular muscle bundles of the acetabular wall, a mass of circular muscle forms a sphincter located adjacent to the inner surface at the level of the narrow orifice that connects the infundibulum to the acetabulum (Figs. 1, 2). A secondary sphincter is also evident near the junction between the outer surfaces of the walls of the acetabulum and infundibulum and has a cross-sectional area that is approximately 10% of the area of the primary sphincter.

The meridional muscle fibers project from a point near the apex of the acetabular roof toward the sphincter muscles as an array of flat bundles that lie between the radial muscle fibers. When the outer surface of the acetabular roof is viewed in a grazing frontal section, the meridional muscle fiber bundles appear to be arranged in a stellate pattern (Fig. 4). Many of the meridional muscle fibers insert on the outer connective tissue layer at the level of the sphincter muscles. Some meridional muscle fibers extend into the wall of the infundibulum.

The arrangement of muscle fibers in the wall of the infundibulum is similar to that of the acetabular wall described above. Radial muscle fibers extend across the wall from their origins and insertions on the inner and outer connective tissue layers of the infundibulum. The radial muscles pass between a series of flat bundles of circular muscle fibers located adjacent to the inner surface of the infundibular wall (Fig. 5). Meridional muscle fibers are also present in the infundibular wall (Fig. 1, Fig. 5). Many originate on the outer connective tissue layer at the level of the sphincter muscles and extend toward their insertion at the margin of the infundibulum while others appear to be extensions of the meridional fibers of the acetabular wall. The bundles of meridional fibers are flat and are interwoven between the radial muscle fibers.

Sucker connective tissue. The two major components of the connective tissues of the sucker are an array of crossed connective tissue fibers embedded in the musculature of the acetabular roof, and the inner and outer connective tissue capsules. Thin layers of connective tissue also surround the circular and meridional muscle bundles of the sucker. It is likely that the connective tissue fibers observed in the sucker are collagenous because

they appear birefringent when viewed with polarized light microscopy and show staining characteristics typical of collagen.

The inner and outer connective tissue capsules are compact layers of fibers that enclose the sucker musculature. The layers appear to be arranged as a crossed-fiber array when viewed in transverse sections that graze the inner or outer surface of the wall (Fig. 6). At the level of the sphincter muscles, fibers of the outer connective tissue layer penetrate into the musculature of the sucker wall (Fig. 5). These fibers branch repeatedly and extend to the primary sphincter muscle, dividing it into fascicles. The extension of the outer connective tissue capsule that encloses the infundibulum is thinner than that of the acetabulum. The inner connective tissue capsule extends from the acetabulum to the infundibulum without any appreciable change in thickness.

In addition to the connective tissue layers encasing the sucker, crossed connective tissue fibers are present in the musculature of the roof of the acetabulum (Figs. 1, 3). These fibers extend between the inner and outer connective tissue capsule at oblique angles to the radial muscle fibers. They are reminiscent of the "intermuscular" connective tissue fibers described by Gosline and Shadwick (1983a, b) and Bone *et al.* (1981) in the mantle of squid and cuttlefish and those described by Kier (1989) and Kier *et al.* (1989) in the fins of squid and cuttlefish. However, the angle they make with the radial fibers is not constant (Fig. 3). These connective tissue fibers do not occur in the acetabular wall. The boundary between the acetabular roof and the acetabular walls includes a particularly robust band of intermuscular connective tissue fibers, and the wall is thinner at this point (Fig. 1).

Sucker epithelium. Several distinct zones of epithelium are present on the sucker (see also Girod, 1884; Guérin, 1908; Nixon and Dilly, 1977; Packard, 1988). The epithelium lining the infundibulum consists of tall columnar cells resting on a basal lamina and the inner connective tissue capsule. These cells secrete a tough, chitinous cuticle (Hunt and Nixon, 1981). The surface of the cuticle bears numerous tiny denticles or pegs, each secreted by a single columnar epithelial cell (see Nixon and Dilly, 1977). The epithelial cells lining the radial grooves of the infundibulum are cuboidal, and the cuticle lining the grooves lacks denticles. The cells of the epithelium lining the acetabulum are cuboidal. In addition, the denticles are rudimentary or absent from the cuticle lining the acetabulum. The transition between the epithelial surfaces of the infundibulum and acetabulum occurs at the level of the primary sphincter muscle (Figs. 1, 2, 5). Another transition is observed in the groove that separates the rim and the infundibulum. The epithelial cells in the groove are cuboidal and the cuticle is thin and lacks denticles. The epithelium covering the pillows and folds of the rim is columnar and the underlying dermis

is loose and folded. An additional differentiation of the epithelium was observed in a zone surrounding the sucker rim. Cells in this zone showed intense staining by Mowry's colloidal iron stain (Humason, 1979) for acid mucopolysaccharides (Fig. 7).

Girod (1884) described the infundibulum of the suckers of *Octopus vulgaris* as being covered by numerous small "hillocks" of tall columnar epithelial cells and cuticle with denticles. He describes the epithelium between the hillocks as being flattened. Although small hillocks are visible on the surface of the infundibulum or on shed sucker linings of the species we examined, no differentiation of the epithelium was observed between the hillocks. A flattened epithelium was only observed in the radial grooves.

Extrinsic sucker musculature. The suckers are attached to the arms by a series of extrinsic muscle bundles (see also Guérin, 1908). A group of major extrinsic muscle bundles is associated with each sucker and originates on the connective tissue sheath surrounding the arm musculature (Kier, 1988) and extends orally to converge on the sucker (Fig. 8). These bundles insert on the outer connective tissue capsule of the sucker at the level of the sphincter muscle (Figs. 1, 2). The extrinsic muscle bundles are, in turn, surrounded along much of their length by a sheet of circumferential muscle fibers (Fig. 8). In addition to the major extrinsic muscle bundles illustrated in Figure 8, a medial group of smaller diameter extrinsic muscle bundles was observed in the region enclosed by the major extrinsic bundles. Although many are oriented parallel to the major bundles, some follow oblique courses, crossing from one side to the other.

Kinematics

Octopus suckers are capable of a wide range of movements. The animals explore their environment with their arms, holding their suckers extended and splayed out. The muscular base that attaches the sucker to the arm can elongate to twice its resting length, extending the suckers away from the arm. Sometimes individual suckers were observed to probe through small openings such as a screen, then extend fully and tilt up and down or side to side. If the sucker is stimulated lightly, it either extends to attach to the stimulus or withdraws, always orienting so that the infundibulum faces the object. When the octopus is active, the infundibuli of the suckers are flattened. Sucker "footprints" in wax show that the entire infundibulum is pressed firmly against the substratum during attachment. When the animal is at rest, the infundibuli are cone-shaped.

An octopus can grip nearly any size object with its suckers. They seem to prefer large flat surfaces but can easily grip irregular objects and objects smaller than their suckers. When manipulating threads or thin sheets, the

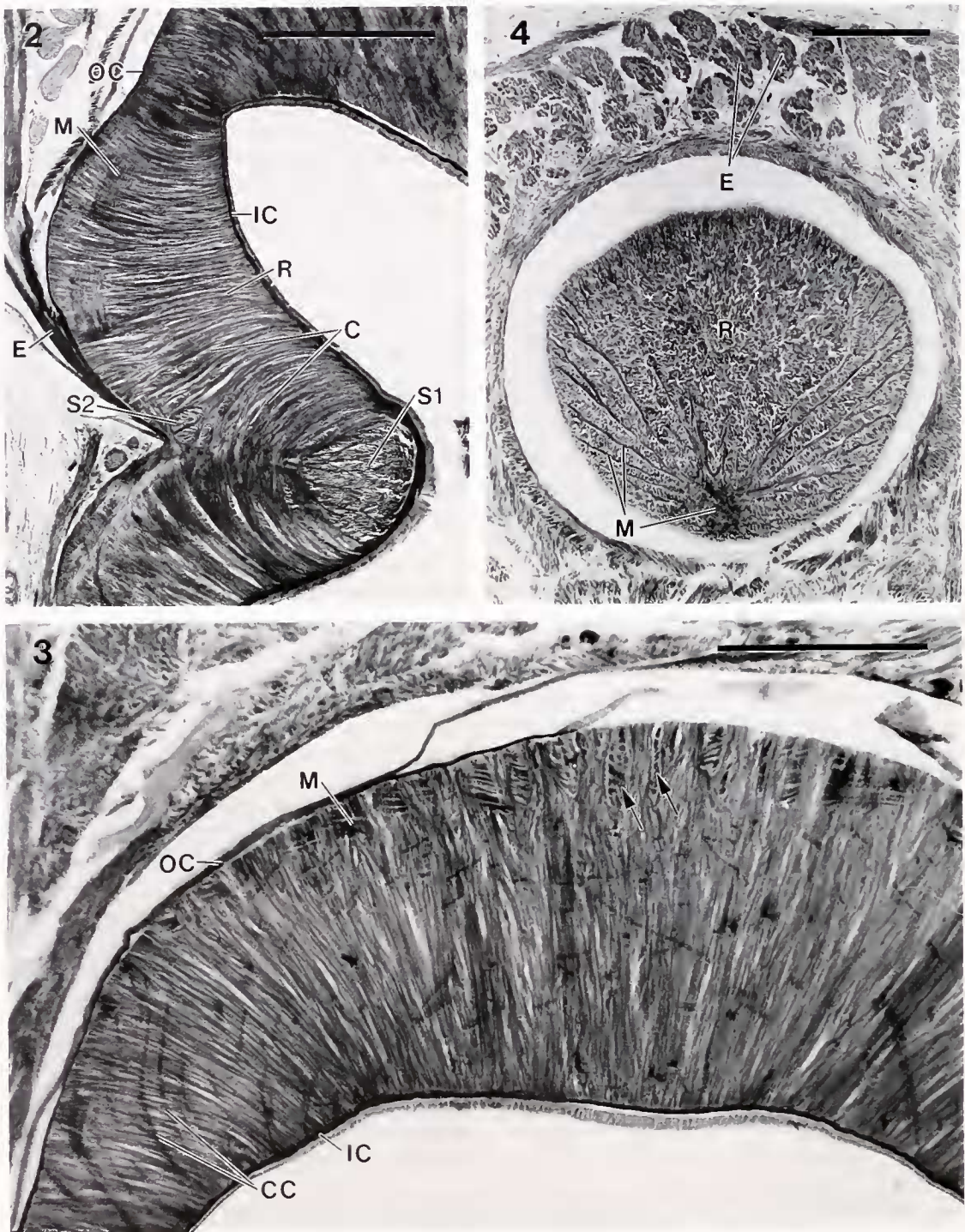


Figure 2. Photomicrograph of a transverse section of a sucker from *Eledone cirrosa* in the region of the primary and secondary sphincter muscles (S1, S2) and the acetabular wall. The radial muscles (R) extend from the inner connective tissue capsule (IC) to the outer connective tissue capsule (OC). Interwoven between the radial muscle fibers are meridional muscles (M) and circular muscles (C). An extrinsic muscle (E) inserts on the outer connective tissue capsule adjacent to the secondary sphincter muscle. The photomicrograph was made using brightfield microscopy of a 15 μm -thick paraffin section stained with Milligan trichrome. The scale bar equals 0.5 mm.

Figure 3. Photomicrograph of a transverse section of a sucker of *Octopus bimaculoides/bimaculatus* in the region of the acetabular roof. The crossed connective tissue fibers (CC) extend across the roof from the inner (IC) to the outer (OC) connective tissue capsule at oblique angles to the radial muscle fibers. Meridional muscle fibers (M) are also visible adjacent to the outer surface of the acetabular roof. The intersection of the meridional bundles at the axis of radial symmetry is apparent in the top of the micro-

suckers sometimes fold so that the two halves of the infundibulum grasp the object like a mittened hand (see also Packard, 1988). A sucker can grip a strand of fishing line and pull on it with surprising force. When it does this, the crease of the fold is usually parallel to the long axis of the arm. Suckers are often observed to fold over the corner of an object without noticeably weakening the force of attachment. A striking example of this occurs when a sucker is attached to the end of a cylinder with a smaller diameter than that of the sucker. Here the perimeter of the infundibulum folds around the side of the cylinder while the remainder of the infundibulum presses flat against the end.

The movies allowed us to distinguish and quantify changes in the sucker's dimensions during suction, particularly the diameter of the large sphincter. We considered the diameter of the orifice leading to the acetabulum to be the same as the diameter of the inner surface of the sphincter. We measured the diameter of the rim and the diameter of the orifice when the sucker was attached (x) and when it was relaxed (x_0). When gripping, the rim diameter increased from its resting state ($x = 1.26x_0^{0.94}$; $r = 0.82$) as does the orifice diameter ($x = 1.48x_0^{0.87}$; $r = 0.80$). The movies also showed that the roof of the acetabulum does not press against the substratum during attachment, contrary to the mechanism reported by Packard (1988).

Discussion

Principles of forming a suction attachment

Suckers attach to the substratum by forming a seal at the rim and reducing the pressure in the acetabular cavity. This decrease in pressure has been measured and can account for all of the attachment force of octopus suckers (A. M. Smith, in prep). The acetabular cavity is filled with water, and the ability of water to withstand this decrease in pressure is critical to sucker function. The distinction between water-filled and air-filled suckers has not been emphasized in previous studies of sucker function (see Denny, 1988).

A sucker filled with air has different mechanical requirements from one that is filled with water. An air-filled sucker must significantly increase its enclosed volume to decrease the pressure in the cavity. Starting from 0.1 MPa ambient pressure (1 atm), doubling the volume

would halve the pressure to 0.05 MPa, increasing the volume ten times would only reduce the pressure to 0.01 MPa. To create a vacuum, the cavity must be reduced to a negligible volume before attachment. The lowest possible pressure inside such a sucker would be a vacuum (0 MPa). At normal ambient pressure (0.1 MPa), the force holding this sucker and the substratum together would be 0.1 MPa multiplied by the area exposed to the vacuum.

Octopus suckers operate in water rather than air, which leads to two important functional consequences: first, the sucker can decrease pressure without detectably expanding, and second, the pressures generated will not necessarily be limited to a vacuum. Water is essentially incompressible at physiological stresses because of its cohesive strength. Therefore, water resists the activity of the muscles that expand the enclosed volume. Thus, if more water does not leak into the sucker, the muscles involved in generating suction contract isometrically, reducing the water's pressure. As long as the water adheres to all surfaces, the sub-ambient pressure in the water pulls the substratum tightly to the sucker. Also, as long as the water adheres to all surfaces, the sub-ambient pressure is only limited by the strength of the water-water bonds. Water columns have sustained pressures as low as -27.0 MPa in the laboratory without breaking (cavitating) (Briggs, 1950). Pressures of this magnitude are extremely difficult to achieve in practice because water does not adhere perfectly to all solid/liquid interfaces. Nevertheless, unlike the situation in air, suckers filled entirely with water have the potential to generate pressures well below 0 MPa. In fact, pressures below 0 MPa have been measured inside octopus suckers (A. M. Smith, in prep).

The difference between air and water has been overlooked in previous work in which octopus suckers were assumed to operate by creating a vacuum (Girod, 1884; Guérin, 1908), or where the pressure was assumed to be limited to a vacuum (Nixon and Dilly, 1977). Parker (1921) measured the suction force from one sucker, but apparently performed this experiment in air, which would explain why he did not measure pressures lower than 0.028 MPa.

The failure to make a distinction between air and water may have led to errors in the literature dealing with such diverse groups as limpets and torrential stream-dwelling vertebrates. Hora (1930) claimed that certain

graph (arrows). The photomicrograph was made using brightfield microscopy of a 10 μm -thick paraffin section stained with Milligan trichrome. The scale bar equals 0.25 mm.

Figure 4. Photomicrograph of a grazing frontal section of the acetabular roof of a sucker from *O. bimaculoides/bimaculatus*. The stellate arrangement of the meridional muscles (M) is visible. The radial muscle fibers (R) and extrinsic muscles (E) appear in cross section in this micrograph. The photomicrograph was made using brightfield microscopy of a 10 μm -thick paraffin section stained with Mallory's triple stain. The scale bar equals 0.25 mm.

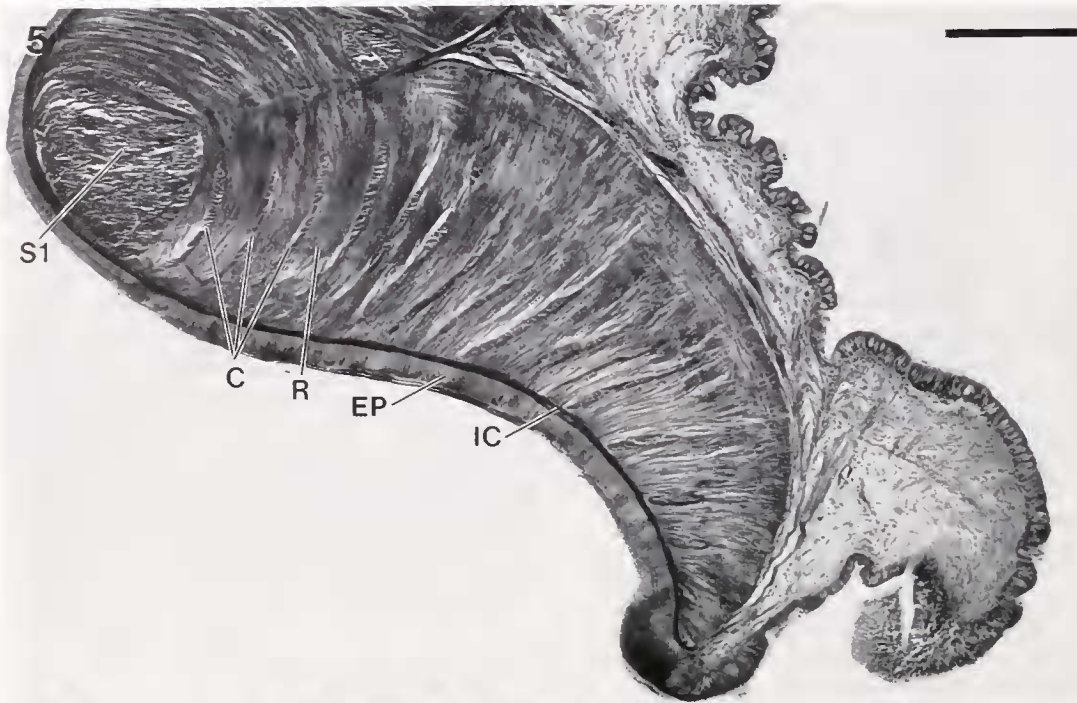


Figure 5. Photomicrograph of a transverse section of a sucker from *Eledone cirrosa* in the region of the infundibulum. The layers of circular muscle bundles (C) are interwoven between the radial muscle bundles (R). The inner connective capsule (IC) underlies the tall columnar epithelium (EP) of the infundibulum. The primary sphincter muscle (S1) is also visible. The photomicrograph was made using brightfield microscopy of a 15 μm -thick paraffin section stained with Milligan trichrome. The scale bar equals 0.25 μm .

Figure 6. Photomicrograph of a grazing transverse section of a sucker from *Octopus bimaculoides/bimaculatus* in the region of the acetabular wall. The connective tissue fibers of the outer connective tissue capsule (OC) are oriented in a crossed-fiber array. Radial (R) and circular (C) muscle fibers of the acetabular wall are also visible. The photomicrograph was made using polarized light microscopy of a 10 μm -thick paraffin section stained with Picro-Ponceau and iron hematoxylin. The scale bar equals 100 μm .

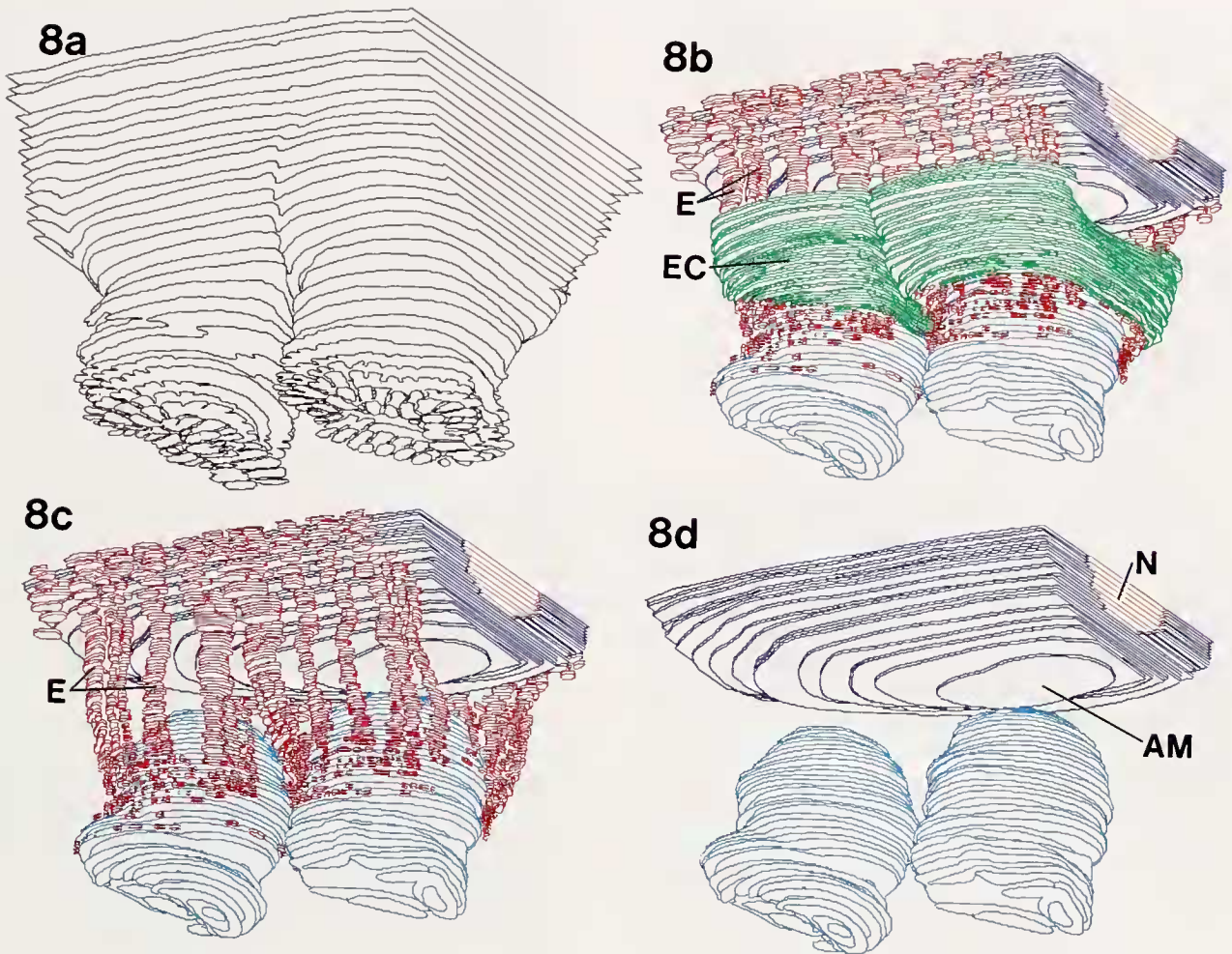


Figure 8. Computer-assisted three-dimensional reconstruction of a portion of an arm of *Eledone cirrosa* showing the extrinsic musculature associated with two suckers. In (a), the outer surface of the arm and suckers is visible. In (b), the epithelium and dermis have been removed to reveal the extrinsic muscles (E) that are surrounded by the extrinsic circular muscles (EC). In (c), the extrinsic circular muscles have been removed to reveal the course of the regularly arrayed extrinsic muscles (E). In (d) the extrinsic muscles have been removed to reveal the arm muscle (AM) and the musculature of the two suckers. The axial nerve cord (N) is also visible.

fish are not using suction because the center of the adhesive disc is not elevated during attachment, as it must be to create a partial vacuum in air. But these suckers are water-filled and therefore there would be no detectable expansion of the cavity while generating sub-ambient pressure. The attachment of limpets has also been attributed to mechanisms other than suction because their tenacity exceeds that which can be explained if one assumes that water cavitates at 0 MPa (Branch and Marsh, 1978; Grenon and Walker, 1981). Seawater can, in fact, endure pressures lower than 0 MPa without cavitating

(A. M. Smith, in prep). Thus, suction attachment mechanisms may be used in both groups.

Another important factor that may have been overlooked is the depth-dependence of the attachment force. The depth at which an octopus lives will have an effect on the relative pressure difference that can be created in the sucker. Just below the surface, the maximum pressure differential is determined by the ambient pressure (approximately 0.1 MPa) outside the sucker and the absolute pressure at which seawater cavitates inside the sucker. With an increase in depth, the ambient pressure

Figure 7. Photomicrograph of a transverse section of a sucker from *O. joubini*. The epithelium surrounding the sucker rim (arrow) shows intense staining of acid mucopolysaccharides. The remaining tissues of the sucker are unstained in this micrograph. The photomicrograph was made using brightfield microscopy of a 10 μm -thick paraffin section stained with Mowry's colloidal iron stain. The scale bar equals 0.25 mm.

outside of the sucker increases while the absolute pressure at which seawater cavitates is unaffected. The potential relative pressure difference increases by 0.1 MPa with every 10 m of depth, rather than doubling as stated by Denny (1988) in his discussion of gas-filled suckers. Since the attachment force of a sucker is the pressure differential multiplied by the area of attachment, the greater pressure differential at depth might allow deep-sea octopuses to create the same attachment force with smaller suckers, assuming that sufficient force can be produced by the sucker musculature. It is of interest in this regard that Voight (1990) has observed an inverse correlation between sucker diameter and depth of occurrence for a variety of octopus species.

Proposed function of octopus suckers

In the following discussion, we propose hypotheses of sucker function, based on the principles of suction attachment outlined above and a biomechanical analysis of the musculature and connective tissue. Further experimental work is required to test these proposals.

Initial contact: forming and maintaining a seal. The first step in generating suction is forming a tight seal to prevent water from leaking in and equalizing the pressure. This implies that the infundibulum must be flexible and dexterous enough to mold itself to a wide range of surface shapes and textures. The infundibulum is composed of a tightly packed three-dimensional array of muscles that allow precise bending. Kier and Smith (1985) outlined the basic principles of this type of system, termed a muscular-hydrostat, and described the wide variety of movements of which it is capable. Since the muscular system itself has a constant volume, contraction in one dimension must be compensated by expansion in at least one other. Contraction of the radial muscles of the infundibulum will thin the infundibulum and thereby extend the rim, increasing the circumference and the surface area facing the substratum. More importantly, the radial muscles can hold the rim extended by resisting the increase in thickness that must accompany retraction of the rim. If the distance from the rim to the primary sphincter cannot decrease when the meridional muscles of the infundibulum contract, the infundibulum will bend toward the arm, flattening the face of the sucker. The circumferential muscles of the infundibulum may function as antagonists to the meridional muscles by constricting the infundibulum to a conical shape. One major advantage the sucker gains by using a muscular-hydrostatic mechanism rather than hard skeletal elements is the local control of movement that is possible. The effect of muscle contraction in the infundibulum is localized such that it can bend at any point. This allows it to match exactly the contours of the substratum. Once matched to the substratum, the mucus and loose epithelium of the rim may provide the seal.

The denticles on the chitinous lining of the infundibulum probably play an important role in maintaining a seal at the rim margin rather than close to the orifice. If the ends of the denticles are resting on the substratum, then an interconnected, water-filled network of spaces will be formed between them. This network may provide a means of transmitting the subambient pressure of the acetabular cavity underneath the entire infundibulum, thereby pulling it tightly against the substratum. The wax impressions of attached suckers demonstrate that the entire infundibulum is forcefully applied to the substratum during attachment. Without such a provision for transmitting pressure, the seal would probably be formed at the orifice and no force would be available to hold the infundibulum against the substratum. This would dramatically decrease the shear resistance of the sucker.

To form an effective attachment, suckers must be able to resist not only forces that lift the sucker away from the substratum but also shearing forces that slide the sucker along the substratum (see Denny, 1988). This is particularly important since the animals appear to prefer holding objects so that the arms are aligned parallel to the force and most of the suckers are thus being sheared rather than being pulled normal to the surface. The friction between the rim and the substratum resists shearing forces and also prevents the rim from sliding towards the center as the pressure in the cavity drops. The denticles on the infundibulum may enhance the friction between the rim and the substratum. As long as the sub-ambient pressure presses the infundibulum against the substratum, the denticles provide a substantial frictional force. In shear, this force determines the tenacity of the attachment. The constant wear from friction may require the sucker linings to be shed periodically.

Some form of denticles or roughened pads often occur on the suckers of other animals. Green and Barber (1988) reported numerous discrete papillae on the marginal region of the sucker of the clingfish. These are covered with a keratin-like cuticle. The authors suggest that these may provide frictional resistance to shear. It is also possible that they allow transmission of the sub-ambient pressure to the rim, as we suggest above for octopus suckers. Denticles or projections are also observed on the surfaces of suckers of other aquatic vertebrates (Hora, 1930; Nachtigall, 1974), lumpsuckers (Arita, 1967), and tadpoles (Gradwell, 1973; Inger, 1966).

Nixon and Dilly (1977) proposed an adhesive function for the denticles on the infundibulum, but they are unclear whether the proposed force comes from capillarity or suction. There is no evidence that the denticles alone are adhesive. Our analysis suggests that only the musculature and connective tissue of the acetabulum are needed to generate the attachment force (see below).

Also important for initial contact are the extrinsic muscles that move and orient the entire sucker. Our me-

chanical analyses predict the following functions for these muscle groups. The major extrinsic muscles link the sucker to the arm, transmitting the force of attachment. They also retract the sucker. The band of extrinsic circular muscles surrounding these dorsoventral muscles will extend the entire sucker away from the arm by thinning the base that connects the sucker to the arm. Simultaneous contraction of both sets of muscles will tilt the sucker, depending on the location of the active dorsoventral extrinsic muscles relative to the axis of rotation. If the circumferential muscles did not provide resistance, the major extrinsic muscles would only retract the sucker.

The primary sphincter muscle probably serves an important function in maintaining suction. As previously suggested, the extrinsic muscles transmit the force of attachment to the arm. These muscles converge from their origin on the arm to insert adjacent to the sphincter. Thus, in transmitting force to the arm, the extrinsic muscles also tend to increase the diameter of the sphincter. During attachment, the diameter of the orifice was observed to increase. Contraction of the sphincter restricts the extent of this increase. If the sphincter could not resist the increase, then the sucker would deform and probably lose its grip. Interestingly, Guérin (1908) stated that pelagic octopuses in the family *Alloposidae* lack a primary sphincter. His figure illustrating a histological section of an allopsid sucker does not show any large extrinsic muscles, only diffuse connective tissue. Another pelagic octopus, *Japattella diaphana*, appears also to lack both primary sphincter muscles and large extrinsic muscles (Nixon and Dilly, 1977). The coincident lack of a primary sphincter and large extrinsic muscles would be predicted if the sphincter serves to resist deformation from the stress of muscles that connect the sucker to the arm.

Sub-ambient pressure generation. Although the infundibulum is critical for making the initial contact, it is the muscles of the acetabulum that probably create the sub-ambient pressure required for attachment. The radial muscles are arranged such that their contraction would increase the enclosed volume, were it not for the resistance of the water. Contraction of the radial muscles of the acetabulum generates a force that tends to thin the wall. Because the wall has a constant volume, a decrease in thickness must increase the internal surface area, or overall size, of the hemisphere and cause the cavity to expand. The cavity cannot expand, however, because of the resistance of the enclosed water. In resisting this expansion, the water is put in tension. The muscular-hydrostat mechanism of the sucker allows suction attachment to occur even if no force is being transmitted from the arm to the sucker. Indeed, the suckers of amputated arms can still attach strongly (Rowell, 1963) as can isolated suckers (Parker, 1921).

The circumferential muscles and meridional muscles of the acetabulum probably function as antagonists to

the radial muscles. Contraction of the circumferential muscles alone would decrease the circumference and increase the height of the acetabulum. Contraction of the meridional muscles alone would decrease the height of the acetabulum. When the sucker is not attached, their simultaneous contraction evenly decreases the hemisphere volume and thereby thickens the cavity wall. The arrangement of radial, meridional, and circumferential muscles in the wall of the acetabulum appears typical of most of the suckers from a variety of phyla as described by Niemiec (1885).

An important aspect of sucker morphology that has been overlooked previously is the array of crossed connective tissue fibers in the musculature of the acetabular roof. Gosline and Shadwick (1983a, b) described an array of crossed connective tissue fibers in the mantle of squid and showed that it could serve as an elastic energy storage mechanism during locomotion and mantle ventilation. Perhaps the connective tissue fibers in octopus suckers also store energy. This elastic energy could maintain sub-ambient pressure in the sucker over extended periods of time, which might account for the observation that octopuses often hold onto objects for several hours. Prior to attachment, the connective tissue fibers of the acetabular roof could be prestrained by the thickening of the acetabular muscle mass that is created by the activity of the meridional and circumferential muscles. Then, upon attachment, the stored strain energy might exert a force analogous to that created by the radial muscles. Thus, rather than expending energy by contracting the radial muscles to maintain suction, suction could be maintained by virtue of the elastic properties of the connective tissue fibers. Nevertheless, several aspects of the arrangement of the connective tissue fibers are perplexing in the context of this mechanism. For example, it is unclear why the acetabular wall lacks these fibers and why the fiber angle is not more regular. Further work is needed to clarify the function of the crossed connective tissue fibers.

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